FACTORS AFFECTING THE DISTRIBUTION OF PAVEMENT ANTS (HYMENOPTERA: FORMICIDAE) IN ATLANTIC COAST URBAN FIELDS[1]

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ABSTRACT: This study shows that disturbance allows the pavement ant to thrive on the Atlantic Coast. Disturbance creates open, dry habitats similar to the habitats occupied by the pavement ant in its native Eurasia. Disturbance tends to minimize competition by creating habitats too harsh or transient for native species. While the pavement ant can encounter competition in these harsh conditions, we note that the pavement ant competes well in urban fields that are abundant in food resources.

The pavement ant, *Tetramorium caespitum* (L.), inhabits open, dry areas throughout much of temperate, mesic Eurasia (Abe, 1971; Brian. 1979; Baroni-Urbani, 1970; Tarzinskii, 1991; Woyciechowski, 1985). The species typically occurs in species-poor habitats, where its large colonies collect a high percentage of available food resources (Abe, 1971; Brian, 1979).

Two hundred years after its probable introduction into North America (Brown, 1957; Weber, 1965), *T. caespitum* is among the most abundant ant species in urban and highly developed suburban areas along the Atlantic Coast (Bruder and Gupta, 1972; Nuhn and Wright, 1979). Despite its prevalence, no study has examined the ecology of this species in North American urban ecosystems.

This study attempts to understand how *T. caespitum* fits into the ecology of urban ecosystems on the Atlantic Coast. To accomplish this, the authors correlated its distribution with physical and biological parameters, observed its ability to compete with native species for large food finds, and followed the progress of thirty-one colonies in a large, minimally disturbed field.

MATERIALS AND METHODS

Data were collected from several fields scattered throughout the northeastern section of Philadelphia, Pa.

Competition for large food finds

In June, 1993, twenty-four cracker baits were placed in vegetation less than 50 cm tall; sixteen in small clearings (<1M^2) in vegetation higher than 50 cm; and nineteen in continuous vegetation higher than 50 cm. Each bait was checked

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at half hour intervals from 4:00 PM (placement) to 6:30 PM (finish), with the species on each bait noted. Sundown occurred at 8:30 PM.

In May, 1995, the process was repeated in low vegetation using twenty-one beef cat food baits. Sundown occurred at 8:00 PM.

Variables affecting soil moisture and temperature

Vegetation: At two hundred thirty-nine random points in ten open fields, the vegetation was measured to determine if it was high (>50 cm), low (< 50 cm), dense (> 50% shade) or bare (< 50% shade). The ant species foraging at each site and the expanse of similar conditions were also noted. All observations were made between 4:00 PM and 8:00 PM in late June, 1993.

Inclination of soil: At 216 of the 239 sites in the above vegetation study, a protractor was used to measure the inclination of the ground to the horizontal.

Soil texture: At eighty sites in areas of low vegetation, surface soil samples were taken to approximate percentages of sand, silt, and clay using the methods described by Stevenson and Talbot (1975). Notes were taken as to the activity of *T. caespitum* at each point where a soil sample was collected.

Tracking of thirty-one *Tetramorium caespitum* colonies

The progress of thirty-one colonies of *T. caespitum* living in a two-plus hectare field was qualitatively followed from the summer of 1991 to the spring of 1995. This was done to add perspective to the other data.

RESULTS

Competition for large food finds

Of the species that foraged on bare ground or in low vegetation, *T. caespitum* and *Monomorium emarginatum* Dubois were clearly dominant. This dominance was as impressive in 1995 as it was in 1993. Combining the data, the two species discovered or co-discovered the forty-five baits a total of forty-three times. Although nine other species competed for baits in low vegetation, *T. caespitum* (with twenty baits) and *M. emarginatum* (with eighteen baits) exclusively controlled eighty-four percent of baits two hours after placement. The two species overwhelmed the competition by finding the baits quickly, and rapidly recruiting dozens to hundreds of foragers to the bait site.

Despite its success in low vegetation, *T. caespitum* was not present at any baits placed in higher vegetation.

Vegetation

Chi squared analysis showed that *T. caespitum* was not randomly foraging in the study fields ($p < .005$, d.f. = 11). Instead, while the species was absent in the dense/high vegetation, it was foraging in 57% of the bare/low sites, 45%

of the bare/high sites, and 34% of the dense low sites. Further chi squared analysis showed that *T. caespitum* preferred sites where the vegetation remained unchanged for thirty or more square meters ($p > .995$, d.f. = 2) .

Inclination of soil

T. caespitum most commonly nested in level soil. The species did, however, show a statistically greater tendency to nest on inclined soil than would have occurred if their distribution was random ($p > .995$, d.f. = 3).

Soil texture

T. caespitum did not prefer specific surface soil textures within our eighty samples. The soils were mostly sandy loam, with organic matter rare or absent. These results were consistent with the Urban Land and Urban Land - Howell Complex Soils found in the study fields (USDA, 1975).

Species present with *Tetramorium caespitum*

When *T. caespitum* foraged with other species, *Lasius neoniger* Emery was the most common (28% of *T. caespitum* containing sites). *M. emarginatum* was next (27%), followed by *Paratrechina faisonensis* (Forel) (21%), *Tapinoma sessile* (Say) (17%), and *Formica* species (15%). Eighteen species cohabited at least once with *T. caespitum.*

In sites that contained *T. caespitum*, thirty percent had *T. caespitum* as the sole species. This made *T. caespitum* the most likely to forage without competition. When foraging with competition present, *T. caespitum* was the most likely to compete against only one species.

Tracking of thirty-one *Tetramorium caespitum* colonies

Of the thirty-one colonies mapped in 1991, twenty-one continued to exist in 1995. Nine of the ten "lost" colonies had vegetation schemes shift from bare/low to dense/high. Three other colonies moved their location approximately five meters when the original site changed from bare/low to dense/high vegetation. The new site was bare/low in all three cases.

Colonies that survived typically inhabited "islands" of year-round sparse vegetation measuring thirty or more square meters in area. The presence of large, flat rocks appeared to correlate with healthier colonies. Colony death routinely occurred when vegetation grew too high and dense.

DISCUSSION

As in Eurasia, *T. caespitum* inhabited the hottest, driest soils found in an otherwise mesic habitat. The species was found in large areas of sparse or low vegetation, where sunlight and wind heat and dry the soil. The species selected inclined soil when available, as inclined soil dries quickly due to run-off and thin vegetation. The soils sampled were "urban", with much fine sand but little organic matter or clay. While these soils are fertile, the combination of sparse vegetation, often inclined ground, and urban soils created relatively xeric conditions in an area that normally is mesic and richly vegetated (Akin, 1991; Godfrey, 1980).

Disturbance often creates species-poor habitats. This occurs because many species either cannot survive the disturbed conditions, or they cannot find these areas before regeneration occurs. As *T. caespitum* finds newly disturbed areas quickly, the species can maintain its large colonies by monopolizing resources due to the absent or minimal competition. The data show that minimal competition is very common for *T. caespitum* in Philadelphia, and this minimal competition resembles the ecosystems *T. caespitum* occupies in Eurasia.

Despite its success in areas of minimal competition, much data show *T. caespitum* competing well in areas of diverse competition. *T. caespitum* had overlapping territories with eighteen species, and twenty-six percent of *T. caespitum* colonies competed against two or more native species. In competition for baits, *T. caespitum* extirpated nine species to gain control of forty-four percent of baits placed in sparse vegetation. *T. caespitum* was a prominent species in a high percentage of areas with sparse vegetation, and species competition did not appear to affect *T. caespitum* while vegetation remained sparse.

We suspect, however, that the result of species competition varies with the amount of food in a habitat. Areas rich in food should favor the large colonies of *T. caespitum*; areas with limited food supplies should favor the much smaller colonies of native competition. Urban fields should possess abundant food supplies, as they contain both human trash and numerous insects killed by pedestrians, passing cars, lawn-mowers, and streetlights. We speculate that both sparse vegetation and adequate resources are needed by *T. caespitum*, but vegetation becomes the active limiting factor in resource-abundant urban areas.

In many ways human disturbance provides acceptable conditions for *T. caespitum*. We have seen that disturbance creates large open, dry areas needed by the species. We have seen that *T. caespitum* finds many disturbed habitats where it competes against little or no native competition. We even speculate that disturbance provides abundant food supplies that should favor the very large colonies of *T. caespitum*. Disturbed areas fill a substantial fraction of *T. caespitum*'s Atlantic Coast range (Boston to Charlotte), and these areas continue to grow in size. This implies that *T. caespitum* may become an increasingly common species in this region of the country.

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